Patterns of exclusion in an intraguild predator–prey system depend on initial conditions

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Summary

1. When intraguild (IG)-prey are superior to IG-predators in competing for a shared resource, theory predicts coexistence of the IG-prey or the IG-predator with the resource depending on the productivity level: (a) resource and IG prey coexist when productivity is low; (b) IG-predator and resource coexist at high productivity; (c) if IG-prey and IG-predators can coexist, it is only at intermediate productivity levels.

2. We tested the existence of productivity-dependent regions of coexistence using an experimental system of two predatory mites and a shared food source (pollen).

3. At high levels of pollen supply (i.e. high productivity), the IG-predator excluded the IG-prey in most, but not all, cases. The same pattern of exclusion was observed at low productivity, at which the IG-prey was expected to exclude the IG-predator. Therefore, species composition could not be predicted by productivity levels. Instead, our results show that initial conditions affected strongly the outcome of the interaction.

4. We emphasize the need for theory on IG-predation that takes the effects of stage structure, initial conditions and transient dynamics into account.

Key-words: community structure, Phytoseiidae, predator–prey dynamics, predatory mites, transient dynamics

Introduction

Omnivores are species consuming resources at different trophic levels (Pimm & Lawton 1978). The simplest food web with omnivory is one with intraguild predation, and consists of a basal resource and two resource consumers, one of which also consuming the other (Polis, Myers & Holt 1989; Holt & Polis 1997). Omnivory, and intraguild predation in particular, were viewed initially as a rare interaction with little effect on food web dynamics (Pimm & Lawton 1978). This view was caused partly by the theoretical prediction that omnivory and intraguild predation destabilize food web dynamics and could therefore not be important. This led to a paucity of studies of this interaction. Because it has become clear that intraguild predation is by no means rare in food webs (Polis *et al*. 1989; Polis & Holt 1992; Rosenheim *et al*. 1995; Polis & Winemiller 1996), it has received considerable theoretical attention (Polis & Holt 1992; Holt & Polis 1997; Morin 1999; Diehl & Feißel 2000, 2001; Mylius *et al*. 2001; Kuijper *et al*. 2003).

Theory on intraguild predation (IGP) predicts possible coexistence of all three species only if the intermediate consumer (intraguild prey, IG-prey hereafter) is superior to the other consumer (IG-predator hereafter) in competing for the shared resource (Holt & Polis 1997). If so, the equilibrium community structure varies along a productivity gradient (Polis & Holt 1992; Mylius *et al*. 2001; Holt & Polis 1997; Diehl & Feißel 2000). At low productivity levels, only the IG-prey persists with the resource because it is the superior competitor and because the IG-prey is not abundant enough to sustain a population of IG-predators. At high productivity, the IG-prey is always excluded, independent of initial conditions. At intermediate productivity levels, predictions depend on the type of functional response (Holt & Polis 1997). As our test animals have type II functional responses (Sabelis 1992; van Rijn *et al*. 2005), we present predictions only of models with such functional reponses. These models show bi-stability at intermediate productivity levels, with either all three species coexisting or the IG-prey being excluded (Holt & Polis 1997; Mylius *et al*. 2001).

Empirical tests of these patterns of coexistence and exclusion at different productivity levels are scarce. Experiments with

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aquatic systems involving protists showed that community structure indeed depends on productivity, although not always as predicted by theory (Lawler & Morin 1993; Morin 1999; Diehl & Feißel 2000, 2001). These deviations from theory were attributed to the limited parameter space for coexistence in this particular experimental system, stochastic extinction during the phase of transient dynamics or accumulation of toxic waste products. Furthermore, the basal resource consisted of several species, which could give rise to complex dynamics at the resource level and thereby could affect higher trophic levels (Diehl & Feißel 2001; Janssen *et al.* 2007).

Here, we test IGP theory in a terrestrial system composed of two predatory mite species: *Iphiseius degenerans* (Berlese) and *Neoseiulus cucumeris* (Oudemans). These two species are used currently as biological control agents of thrips in greenhouses (van Houten & van Stratum 1995), and co-occur in the Mediterranean area (De Moraes *et al.* 2004). In this system, *I. degenerans*, the IG-predator, preys on all mobile juvenile stages of *N. cucumeris*, the IG-prey, whereas eggs and adults of *N. cucumeris* are invulnerable, and both species are capable of feeding and reproducing on several types of pollen (van Rijn & Tanigoshi 1999). In the experiments presented here, we used cattail pollen (*Typha* sp.) as the shared resource. The amount of pollen was varied to create different productivity levels and it was supplied at regular intervals to simulate resource dynamics.

We first tested whether our system matched the conditions under which theory predicts such patterns of coexistence and exclusion, i.e. that the IG-prey (*N. cucumeris*) is superior to the IG-predator (*I. degenerans*) at exploitative competition for the shared resource (pollen). Secondly, we tested whether intraguild predation occurred in presence of the shared resource. This is carried out because many species engage in intraguild predation only the in absence of other food sources, which reduces the system effectively to one of resource competition. Finally, we conducted competition experiments at different resource densities to assess whether the patterns of exclusion or coexistence in our experimental system matched those predicted by IGP theory.

Materials and methods

STOCK CULTURES

The origin and culturing methods for both species are described in van Rijn & Tanigoshi (1999). Both species were reared on plastic arenas placed on top of sponges in water-containing trays. The edges of the arenas were covered with tissue paper that was in contact with the sponge and the water, serving both as barrier and water source. *Iphiseius degenerans* was fed birch pollen (*Betula pubescens* Ehrh.) and *N. cucumeris* cattail (*Typha* sp.) pollen, both twice per week.

Pollen was collected from *Typha* sp. and birch plants at the campus of the University of Amsterdam. Male flowers were dried in a stove at 45 °C for 24 h, then sieved (350 μm). The pollen was stored subsequently in a freezer (–10 °C) until use.

TESTING THE MODEL ASSUMPTIONS

Exploitative competition for the shared resource

The goal of this experiment was to assess whether the IG-prey (*N. cucumeris*) was superior at exploitative competition for the shared resource, cattil pollen, i.e. whether it would persist at a resource level at which the IG-predator would go extinct. Experiments were carried out on plastic arenas (14·5 × 7·5 cm) placed on top of sponges that were inside water-containing plastic trays, with margins covered with tissue paper as above. Arenas were supplied with either $4·8 × 10^{-3}$ g (high) or $8 × 10^{-4}$ (intermediate) g of pollen twice per week. Ten gravid females of either the IG-prey or the IG-predator (9–11 days old since egg deposition) were introduced onto the arena. The number of adults, juveniles and eggs were counted twice per week until a maximum of 50 days, which corresponds to approximately five generations (the time from egg to egg is approximately 9 days – M. Montserrat, personal observation). After counting, the pollen remaining in the arena was removed with a wet brush, and replaced with fresh pollen. There were two replicates per level of pollen supply.

Intraguild predation in presence of the resource

Many species only engage in intraguild predation in absence of other food sources, whereas most models assume that the IG-predator feeds simultaneously on the IG-prey and on the shared resource (but see Krivan 2000 and Krivan & Diehl 2005). Therefore, predation of the IG-predator on the IG-prey in presence or in absence of the resource (pollen) was assessed. The experiment was carried out on plastic arenas (7·5 × 7·5 cm) that were otherwise similar to those described above. One female *I. degenerans* and 30 juvenile *N. cucumeris* (3–4 days old since egg deposition) were added to each arena, either with or without an ample supply of cattail pollen. After 24 h, the number of juveniles eaten and the number of eggs laid by the female predators were counted, and new juveniles were added to the arena to adjust their number to 30. Twenty-four hours later, dead juveniles and eggs laid by the female were counted again. Arenas with 30 juvenile IG-prey without IG-predator were used as a control for natural mortality, and controls for oviposition consisted of arenas with one *I. degenerans* female with pollen only. Ten replicates were performed for each treatment.

Predatory mites lay two to three eggs per day (van Rijn & Tanigoshi 1999) and they can produce only one egg at a time (Faraji, Janssen & Sabelis 2002). Consequently, the first egg laid by females during the first 24 h of the experiment could still be produced from food obtained prior to the experiment. To ensure that only the effect of the treatment was measured, only data of the second day were analysed. The number of dead juveniles (log-transformed) was subjected to a two-factor analysis of variance (ANOVA), with presence of a predator and presence of pollen as main factors. The number of eggs laid by the female predatory mites was subjected to a one-factor ANOVA, with type of diet as factor. Means were compared using the Tukey least squares difference (LSD) test.

TESTING INTRAGUILD PREDATION THEORY

Experiments were carried out on 14·5 × 7·5 cm plastic arenas, similar to those described above. A strip of filter paper was placed on the middle of the arena separating the arena in two halves. Ten

gravid females of *I. degenerans* were added to one half of the arena, and 10 gravid females of *N. cucumeris* to the other. To prevent the two species from mixing, a line of insect glue (Tanglefoot®, Grand Rapids, MI, USA) was applied on top of the strip of filter paper. An ample amount of cattail pollen was added to both sides of the arena. Six days later, the number of adults, juveniles and eggs of both species were counted and the pollen remaining on the arena was removed. By this time, all the developmental stages of the two species were present on the arenas. The strip of filter paper was then removed, thus allowing the two species to mix. Productivity levels were created by supplying arenas twice per week with either high or intermediate amounts of pollen as above. Finally, the number of adults, juveniles and eggs of both species were counted twice per week for a maximum of 60 days, or until one of the species went extinct. After each count, the pollen remaining in the arena was removed with a wet brush and replaced with fresh pollen. There were four replicates per treatment.

Unexpected results obtained in the experiments at the intermediate pollen density (see Results) prompted us to conduct similar experiments at even lower levels of pollen supply. Two replicates with a mixed population of the two species of mites, supplied with 10^{-4} g of pollen twice per week (low pollen supply), were performed. In addition, one replicate with the IG-prey only was performed to test for its persistence at this resource density. To analyse whether the initial conditions affected population dynamics, two replicates were first performed of an experiment with arenas supplied with either intermediate or low pollen supply twice per week, in which the initial numbers of the IG-predator introduced onto the arena were three instead of 10; secondly, four replicates were carried out in which a single female of the IG-predator was introduced into a population of IG-prey with intermediate pollen supply, thus mimicking an invasion event. If the IG-predator failed to establish, single females were introduced repeatedly to account for failures due to stochastic events. In all cases, populations of the IG-prey were allowed to establish for three weeks on the arena with an intermediate supply of pollen prior the introduction of the IG-predator.

Results

TESTING THE MODEL ASSUMPTIONS

Exploitative competition for the shared resource

The IG-prey reached much higher densities than the IG-predator at the highest pollen density tested (Fig. 1). At intermediate pollen densities, only the IG-prey persisted at constant densities, whereas the IG-predator went extinct (Fig. 1). These results indicate that the IG-prey is the superior competitor for the resource.

Intraguild predation in presence of the resource

Females of the IG-predator killed a large number of IG-prey protonymphs when compared to protonymph mortality in absence of IG-predators ($F_{1,36} = 381 \cdot 48$, $P < 0 \cdot 0001$, Fig. 2a). The presence of pollen did not affect the predation rate on these protonymphs ($F_{1,36} = 3 \cdot 83$, $P = 0 \cdot 058$, Fig. 2a), but the oviposition rate was higher in the presence than the absence of pollen ($F_{2,27} = 11 \cdot 11$, $P = 0 \cdot 0003$, Fig. 2b).
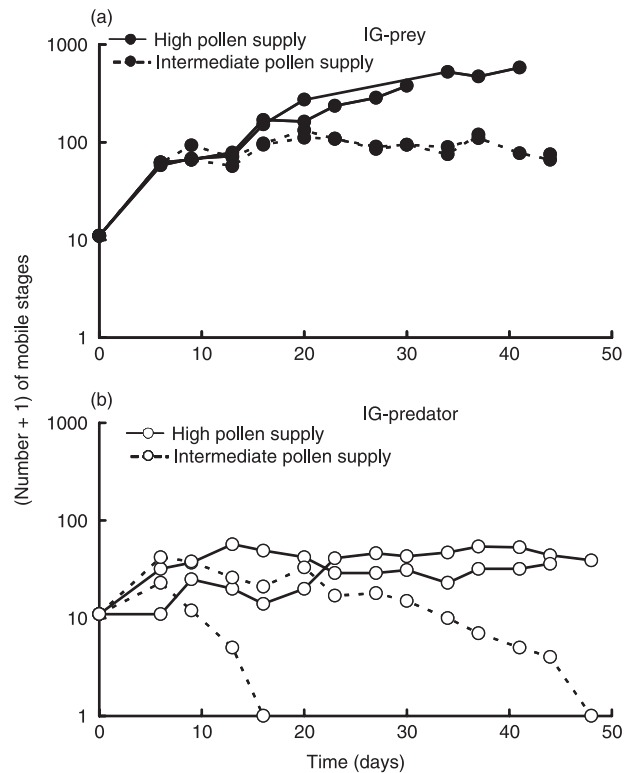

Fig. 1. Population dynamics of the intraguild (IG)-prey *Neoseiulus cucumeris* (a) and the IG-predator *Iphiseius degenerans* (b) when supplied twice per week with high ($4 \cdot 8 \times 10^{-3}$ g) amounts (solid lines) or intermediate (8×10^{-4} g) amounts (dotted lines) of pollen.

TESTING INTRAGUILD PREDATION THEORY

As was expected at high productivity levels, the IG-predator excluded the IG-prey at the highest pollen density tested, but only in three of four replicates (Fig. 3). Hence, the exclusion of the IG-predator in the fourth replicate was unexpected (Fig. 3d).

At intermediate pollen supply, at which the IG-predator could not persist with the resource (Fig. 1b), the IG-prey excluded the IG-predator in one replicate (Fig. 4a). This result is in agreement with theoretical expectations. Contrary to expectations, the IG-predator excluded the IG-prey in the other three replicates (Fig. 4b–d). Although the populations of the IG-predator were not followed further after the IG-prey was excluded, experiments with IG-predators and shared resource only indicate that the IG-predator would also have gone extinct after eradication of the IG-prey (cf. Fig. 1). At the lowest pollen density tested, we again observed that the IG-prey was excluded by the IG-predator, which subsequently went extinct (Fig. 5a,b).

To assess whether these unexpected results were due to initial conditions, we changed the initial numbers of IG-predator females prior to joining the two species to three instead of 10. When the amount of pollen supplied was intermediate, both species went extinct almost simultaneously (Fig. 4e,f). However, at a low pollen supply, the IG-prey excluded the IG-predator and increased in numbers (Fig. 5c,d) until it reached the level of a population without IG-predators (Fig. 5e), which is in agreement with theory.
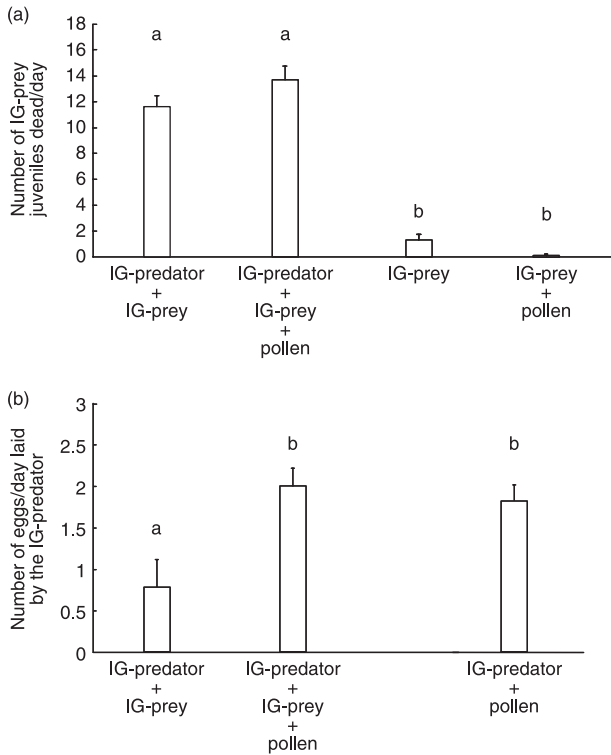
Fig. 2. (a) Number of dead intraguild (IG)-prey juveniles day^{-1} in presence or absence of ample pollen and in presence or absence of the IG-predator. (b): Oviposition rates (eggs day^{-1}) of the IG-predator in presence of the IG-prey, of pollen, or of both. Different letters indicate significant difference among treatments.

To test further the effects of initial conditions, we carried out invasion experiments in which low numbers of IG-predators were added to established populations of the IG-prey at intermediate pollen levels. Based on theory, we expected that the intraguild predator would not be able to invade. This is indeed what was found; repeated introductions of the IG-predator (indicated with arrows, Fig. 6) all failed.
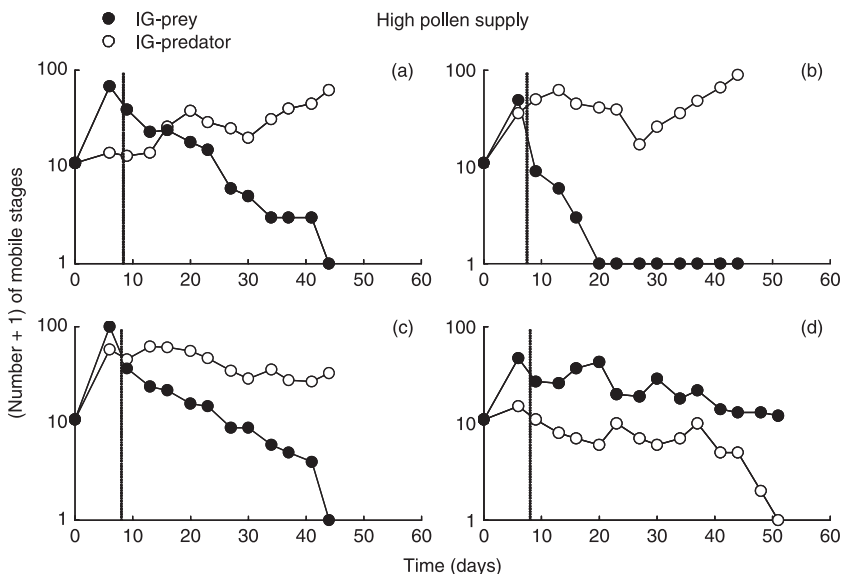
Discussion

Although our system meets the assumptions of theoretical models of intraguild predation (i.e. the IG-prey is the superior competitor for the shared resource; Holt & Polis 1997; Diehl & Feißel 2000; Mylius *et al.* 2001), we failed to find the coexistence and exclusion patterns predicted by theory. In agreement with theory, the IG-predator excluded the IG-prey at the highest resource density, except for one replicate in which the IG-predator was excluded. At intermediate resource levels, at which the IG-predator cannot persist on the resource alone, we would expect either the coexistence of IG-prey and IG-predator or the extinction of the IG-predator (Holt & Polis 1997; Diehl & Feißel 2000; Mylius *et al.* 2001). Exclusion of the IG-predator was, however, observed in only one of four replicates, whereas the other replicates showed unexpected exclusion of the IG-prey or extinction of both species.

How to explain the fact that we found multiple outcomes of the interaction for all productivity levels? This is unlikely to arise from the existence of alternative equilibria. Although theory predicts such alternative equilibria in systems with IGP at intermediate productivity levels, these predictions do not include the possibility of IG-predators excluding IG-prey at productivity levels that are insufficient for IG-predators to persist.

The pattern found here, that either the IG-predator or the IG-prey excluding each other, is predicted by more recent theory in which the IG-predator shows ontogenetic diet shifts (van de Wolfshaar, de Roos & Persson 2006). These authors show mutual exclusion of the IG-predator and IG-prey, with initial conditions determining which species will be excluded. The region in which this mutual exclusion occurs is largely independent of productivity, a pattern that we also observe in our experiments. However, the IG-predator in our system does not show such ontogenetic diet change (M. Montserrat and A. Janssen, personal observation). Other recent theory
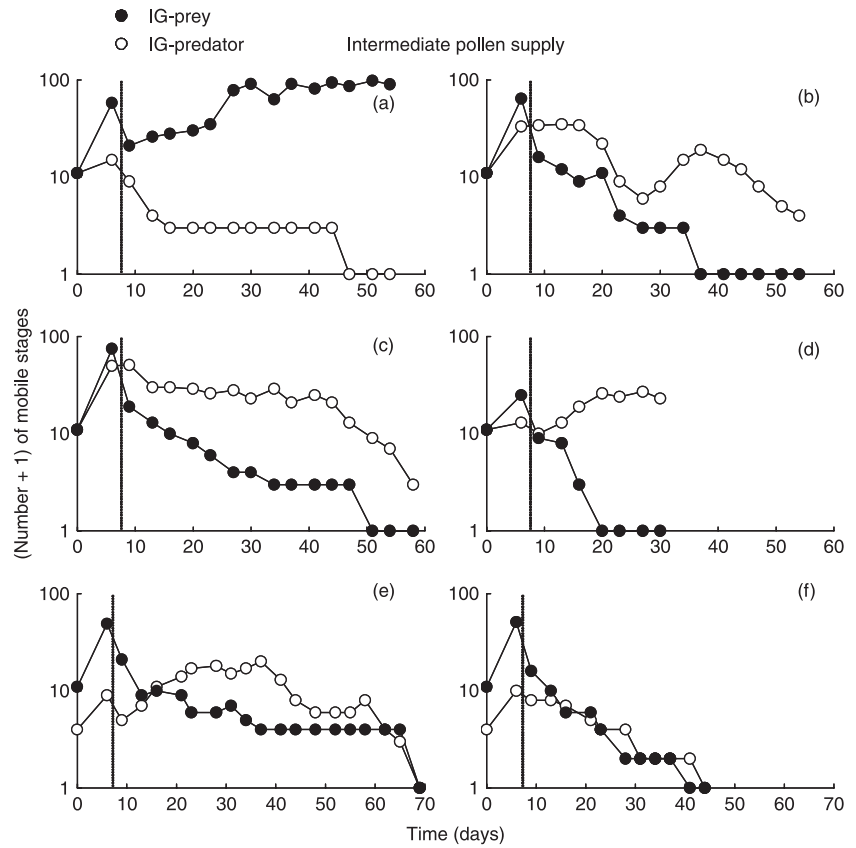

Fig. 3. Population dynamics of the intraguild (IG)-prey (*Neoseiulus cucumeris*, black dots) and of the IG-predator (*Iphiseius degenerans*, white dots) at high pollen supply (4·8 × 10^{-3} g). Vertical lines indicate the moment at which populations of the two species were joined.

Fig. 4. Population dynamics of the intraguild (IG)-prey (*Neoseiulus cucumeris*, black dots) and the IG-predator (*Iphiseius degenerans*, white dots) at intermediate pollen supply (8×10^{-4} g), with the initial numbers of IG-predator and IG-prey females being 10 each (a, b, c, d), or three and 10, respectively (e, f). Vertical lines indicate the moment at which populations of the two species were joined.
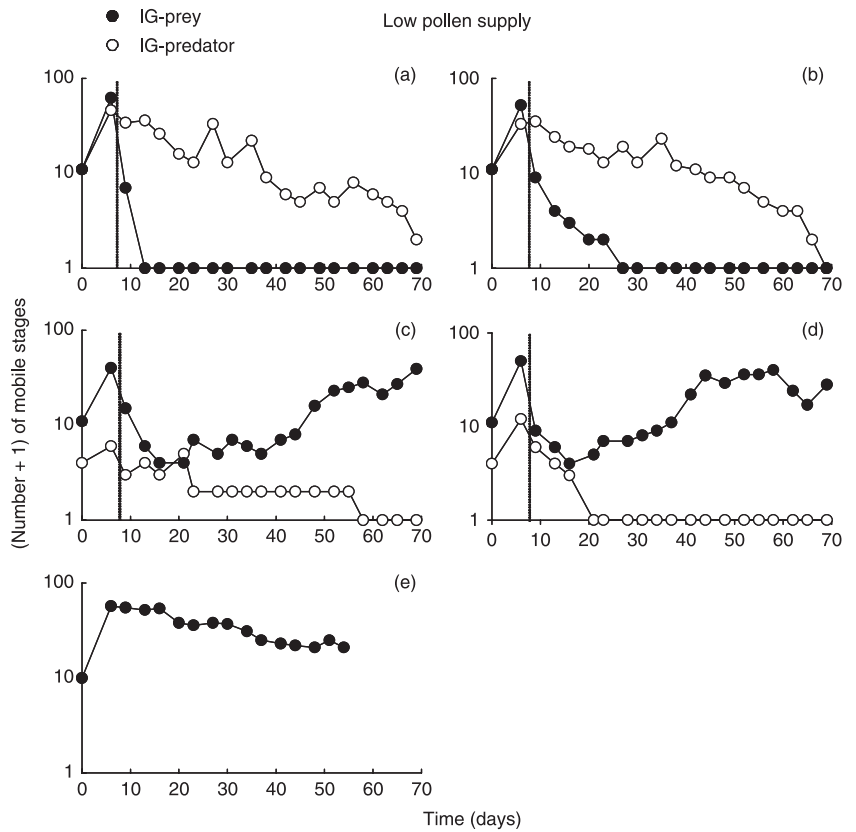

Fig. 5. Population dynamics of the intraguild (IG)-prey (*Neoseiulus cucumeris*, black dots) and the IG-predator (*Iphiseius degenerans*, white dots) at low pollen supply (10^{-4} g), when the initial numbers of IG-predator and IG-prey females introduced onto the arena were 10 each (a, b), or three and 10, respectively (c, d). Vertical lines indicate the moment at which populations of the two species were joined. The population dynamics of the IG-prey without the IG-predator at low pollen supply is shown in (e).
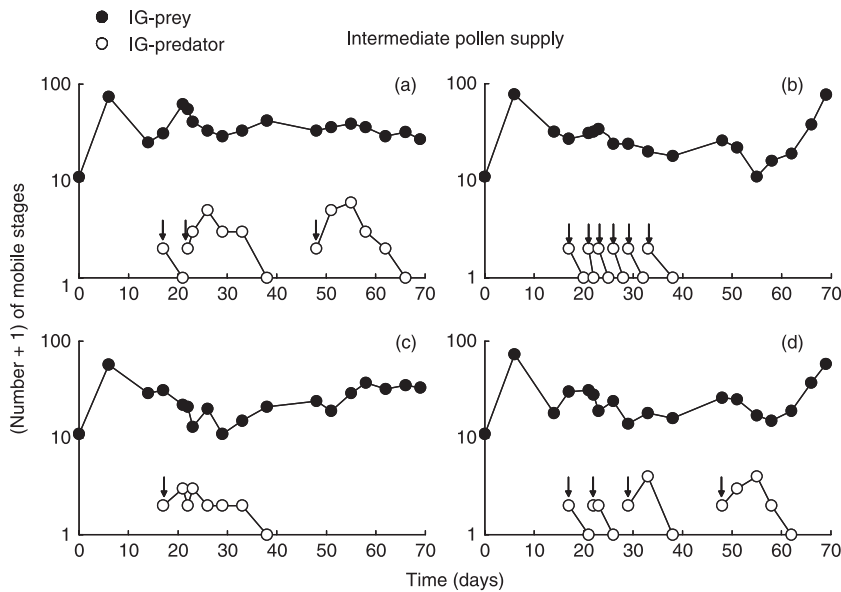
Fig. 6. Invasion dynamics of the intraguild (IG)-predator (*Iphiseius degenerans*, white dots) into a population of the IG-prey (*Neoseiulus cucumeris*, black dots) with intermediate (8×10^{-4} g) pollen supply. Arrows indicate successive introductions of one single female of the IG-predator.

shows that coexistence of IG-prey and IG-predators is limited when the two predators are engaged in reciprocal intraguild predation, with IG-prey adults feeding on IG-predator juveniles (HilleRisLambers & Dieckmann 2003). Indeed, predation can be reciprocal in our system, as in many other systems of IGP (cf. Polis *et al.* 1989). This factor could lead to mutual exclusion, with priority effects determining which species will persist. In disagreement with this latter theory, however, is the fact that the IG-predator in our system is capable of excluding the IG-prey at productivity levels that are insufficient for the IG-predator to persist.

Hence, it is clear that our experimental results do not support model predictions. We suggest three possible explanations for this discrepancy. First, stochastic rather than deterministic dynamics during the initial, transient phase of the interaction are an important determinant of our experimental results. There is no theory on stochastic transient dynamics of systems with intraguild predation (Briggs & Borer 2005). In the system studied here effects of stochasticity are unavoidable; indeed, the densities of mites were rather high relative to natural densities. Perhaps experiments with systems that reach much higher densities, such as protists (Lawler & Morin 1993; Morin 1999; Warren, Law & Weatherby 2003) would be more suitable to study effects of stochasticity.

Secondly, our data are on transient dynamics, whereas model predictions are based on equilibrium dynamics. Indeed, it has been argued that transient dynamics in ecological systems are more likely to be the rule than an exception (Hastings 2004; references therein). Such transient dynamics may be highly dependent on initial conditions. Indeed, there is experimental evidence that initial conditions determine which stable community is reached (Warren *et al.* 2003).

Thirdly, it is important to realize that the system studied here differs from most theoretical systems because of the stage structure of the populations of IG-predators and IG-prey. This may be crucial because not all stages of the IG-prey feed on all stages of the IG-prey. Models considering stage-structured populations of both IG-prey and IG-predators are still lacking. Also, other aspects of stage structure such as role reversals (Janssen *et al.* 2002; Magalhães *et al.* 2005) are still not covered by IGP theory and, indeed, many IG-prey also feed on small IG-predators (Polis *et al.* 1989). We suspect that the interplay of initial conditions and stage structure of populations is important for an understanding of system dynamics, because different initial conditions and reciprocal IGP are likely to occur in most IGP systems.

We suggest that the outcome of the interaction between populations of the IG-predator and the IG-prey depend upon initial conditions and stage structure of the populations. Indeed, the IG-prey was always eradicated by the IG-predator when the initial numbers of the IG-predator were high (Figs 4f,c, 5a,b). Hence, the high initial IG-predator populations may have killed all IG-prey during the transient phase, even if IG-predators were expected to be absent at equilibrium under a deterministic scenario (Fig. 1). As shown in Figs 1 and 2, a single IG-predator female killed around 12 IG-prey juveniles per day (irrespective of pollen density), whereas the oviposition rate of the IG-prey at low pollen density was in the order of 1·6 eggs per female per day (unpublished data). Together with a high initial density of the IG-predator, this increases the likelihood of eradication of the IG-prey during the initial phase of the interaction. Indeed, when the initial numbers of the IG-predator were low, the IG-prey excluded the IG-predator in most cases (Figs 4a, 5c,d and 6). Furthermore, comparison of the results at intermediate pollen supply rate show that the outcome of the interaction was more variable with a high initial density of the IG-predator (Figs 4 and 6). At high densities, the stage structure of the IG-predator population was more variable, as was the outcome of the interaction, whereas when the density and the stage structure was kept constant (i.e. one adult female, Fig. 6), the outcome of the experiments was always the same.

Three replicates showed different dynamics from other replicates with similar initial conditions, and they require further explanation: one with the IG-prey being excluded by IG-predator even though initial numbers of the IG-predator were low (Fig. 4d), and two with both the IG-predator and IG-prey going extinct simultaneously (Fig. 4e,f). We suspect that these replicates differed in stage structure from the other replicates, perhaps with different densities of invulnerable IG-prey stages (i.e. adults) and non-predatory IG-predator stages (i.e. juveniles). Such stage structure is predicted to affect coexistence and exclusion patterns (Mylius *et al.* 2001). Unfortunately, our data do not allow further analysis.

In conclusion, our experimental system fulfilled the necessary conditions for the productivity-dependent community shifts that are predicted by theory to be observed, yet our experimental results did not confirm such shifts. In particular, our results suggest that the initial size structure of IG-predator and IG-prey populations may, to a large extent, determine the transient dynamics and patterns of coexistence and exclusion. We suggest that transient dynamics, stochastic events and stage structure of the populations are responsible for this discrepancy and that theory and experiments should focus on this.

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